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Colonisation by ground and edaphic invertebrates of soil patches with different pollution levels

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Key words: colonisation process/terrestrial invertebrates/pollution levels.

Abstract

Background and Purpose: A key aspect of resilience is the ability of a species to recolonize disturbed areas. The re-establishment of fauna in terrestrial systems is a subject that has been investigated for many years, although most studies have been conducted in laboratory conditions or on selected species. Few studies analyzed the process at community-level in the field. We examined the colonization patterns of invertebrate communities after total depletion and in different degrees of soil pollution.

Material and Methods: For this purpose, we established four patches with different environmental conditions: an untreated control area, and three areas where the soil fauna was at first completely depleted by steam sterilization and then three different concentrations of soil pollution were simulated through the addition of pesticides. On five dates (ili On five occasions) we examined the abundance and taxa richness of edaphic microarthropods and ground invertebrates.

Results and Conclusion: Our data show that the abundance and richness of terrestrial invertebrates are strongly related to the presence of a pollution gradient: a high contamination level inhibits the re-establishment of faunal communities, and a low contamination level reduces the entire reinvasion process. We detected a similar pattern of recolonization in both ground and edaphic communities suggesting that above and below terrestrial systems are highly coupled (connected/linked). Our study can be of interest in the assessment of the effectiveness of reclamation measures.

INTRODUCTION

Community resilience is a topic of main (major) interest in ecology, due to its pure and applied implications. The re-establishment of a community after disturbance is a complex process that involves different structural and functional properties, such as the number of taxa, total number of individuals, species composition and relative abundance (i.e. biodiversity). Environmental alterations can deplete or destroy a biocenosis, although normally a recolonisation process begins as soon as conditions are restored (1). Initial theories of ecological succession were initially developed by plant ecologists (2): succession was viewed as an ordered process dominated by autotrophic organisms. In a recent study, Hodkinson *et al.* (3) underlined the importance of heterotrophic organisms in the earliest phase of the recolonization process. In particular, colonisation of newly exposed substrates by invertebrates represents the first important step of the entire ecological succession and allows rapid establishment of simple but functional

ecological communities. Moreover, invertebrates usually represent good indicators of ecological condition because they are highly diverse and functionally important, can integrate a variety of ecological processes, are sensitive to environmental changes and are easily sampled (4).

Investigations of structure, abundance and distribution of soil faunal assemblages have shown that communities are very diverse in taxa richness, highly spatially aggregated and exhibit a relatively low degree of trophic specialisation (5, 6). During the last decades, great efforts have been made to understand the role of invertebrate biodiversity in soil processes (7, 8, 9), their interactions with the abiotic factors of soil function (10, 11, 12), and their importance in biomonitoring studies (13, 14, 15).

Many studies have investigated the recolonisation patterns of invertebrate communities in freshwater (16, 17) or terrestrial habitats (3, 18), but information on soils is still scarce. Even if soil zoology is an indispensable component of integrated ecosystem studies (19), soil is an under-represented medium in dispersal studies, especially when they pertain to truly edaphic fauna in field conditions. The patterns of soil recolonisation after a disturbance has been scarcely studied, with some exceptions related to particular groups, such as mites (20), springtails (21), carabids (22) and spiders (23). Evidence of colonisation patterns among pedofauna elements comes mainly from laboratory observations realized in artificial substrates (1, 24) and, even when some field studies focused on ground macroinvertebrates (23), few or no information is available for both edaphic and ground community colonisation patterns in field conditions.

Many types of disturbances affect soils, such as intensive agriculture (25), grazing pressure (26), deforestation (27), fire (28) and pollution (13). Anthropogenic activities can affect soil animal communities by altering the quality and quantity of detritus and non-detritus input and by influencing the soil microhabitat in terms of soil physical and chemical qualities (29). In particular, soil contamination is one of the major ecological problems in heavily industrialized regions of Europe (30), and for this reason expensive projects of restoration of contaminated sites are starting in different countries.

The success of a reclamation process is the result of many elements and can be very difficult to assess (15). Chemical analyses can establish the presence and concentration of several kinds of contaminants; but also if the reclamation process leads to the level of contamination of each single element under its legal point, the sum of the effects of several chemicals or the persistence of physical alteration may alter the accomplishment of the recovery. This cannot be easily measured with traditional chemical systems, but can be assessed by analysing the soil biota. Disturbance caused by pollutants in the soil results in both qualitative and quantitative changes in invertebrate fauna. For its high sensitivity and synthetic capacity, the use of biological indicators based on fauna populations has attracted growing attention (interest) in

recent years (31). The study of recolonization patterns of soil mesofauna can provide useful information about the effectiveness of contaminated sites reclamation (32). Soil parcels, which are no longer contaminated by toxic materials, are quickly colonized by edaphic fauna (33), while soil parcels with residuals of pollution probably show a slower rate of colonization.

The aim of this study was to investigate the colonization (re-invasion) rate of invertebrates in defaunated patches with different pollution levels. We analysed the rate of recolonisation of edaphic microarthropods (soil mesofauna – from 0.02 to 2 mm) and ground macroinvertebrates (soil macro-fauna – larger than 2 mm). We evaluated the colonisation patterns of invertebrates in relation to pollution levels with an experimental approach, and a two factor sampling protocol:

(1) To evaluate the effects of pollution levels, three 30 m² soil areas were firstly sterilised by steam treatment to completely deplete living invertebrates. Different pollution conditions were then simulated by applying a range of chemical concentrations (NO, low and high). A control area without treatment was also monitored to allow comparison with natural conditions.

(2) To evaluate the effect of time on the colonization process, the three experimental plots were sampled (at different dates) on different occasions.

The relevance of invertebrate colonization studies could be of applicative interest because the resilience of their communities is suitable for monitoring the effectiveness of reclamation activities in previously contaminated sites.

MATERIALS AND METHODS

Experimental design

The study was carried out in Boves, NW Italy (lat. 44°29' N – long. 7°33' E), in a region of extensive agriculture. We conducted experiments in an open-field area by establishing four 5.5 × 5.5 m patches (plots?) with different treatments. In three patches, we first carried out steam sterilisation treatment to deplete the faunal communities. The first patch (NO) was only sterilized without any other treatment, the second patch (LOW) was sterilized and contaminated with a low concentration of chemicals (20 cc of Panter Cyanamid and 10 cc of Sialan in 5 l of water), and the third patch (HIGH) was sterilized and contaminated with a high concentration of chemicals (40 cc of Panter Cyanamid and 30 cc of Sialan in 5 l of water). The fourth patch (C) was a control area without either steam or chemical applications. The quantity of chemical contaminants for the LOW treatment was chosen to simulate the quantity usually employed by farmers in our study area and suggested by the producer. The quantity sprayed on the HIGH patch was about twice the concentration of the LOW patch. Panther Cyanamid is a long permanence cyanate compound, containing Pendimethalin and Linuron: the first is a 2,6 dinitro-aniline herbicide, with inhibitor effect on cell division, the second is a urea compost, with photosynthetic inhibition

effect. Sialan is an organochlorine compound, containing Endosulfan, a non-systemic pesticide with long permanence (duration) and strong effects on insects and mites (34).

Steam sterilisation method

The soil was heated by sheet steaming on the 20th of June 2003. The soil was covered with a thermo-resistant sheet sealed at the edges. Steam was blown under the sheet, so that it penetrated into the soil, by two parallel pipes placed in the trenches between ridges. Each pipe was connected to a valve by which air could be injected through a Venturi inlet. We used a Möschle S500 boiler, that produced about 550 kg/h of steam. During each treatment (lasting two hours per plot), the boiler output was directly connected to the pipes through (by) an on-off valve.

Steam sterilisation is an efficient method to deplete soil microarthropod communities. Indeed the temperatures at 15 cm depth reaches a value of 100 °C and at 40 cm it still remains approximately at 90 °C.

Pedofauna sampling

We collected soil samples in six different dates: before the sterilisation, 8 hours, 10 days, 15 days, 25 days and 40 days after sterilisation. On each occasion, six samples were collected with a soil sampler in NO, LOW, and HIGH patches: two near the edges, two at 1 meter from the edges and two in the centre (Figure 1). On the same date, we also collected three samples in the control C patch.

Each sample consisted in three replicates of a core sample (diameter 7.5 cm; deep 10 cm), with all vegetation residuals cut to ground level so that only the soil fauna was collected. Each sample was placed in a cylindrical screw-top container to protect the core from drying and breaking up before extraction. Microarthropods were extracted with Berlese-Tullgren funnels for 10 days.

The enormous species richness of soil organisms combined with poor taxonomic information makes the revision of soil biota difficult. For this reason, we grouped edaphic microarthropods into 19 broad assemblages (details in Appendix I).

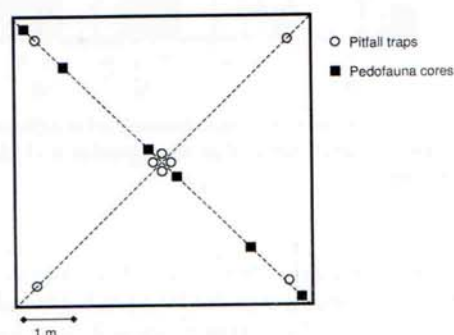


Figure 1. Position of the pitfall traps and of the core soil samples in each of the HIGH, LOW, and NO experimental patches.

Ground invertebrate sampling

To collect surface active and soil associated invertebrates (size > 2 mm) we placed in each patch (NO, LOW, HIGH) eight pitfall traps (Figure 1), and three pitfall traps in the control C area. Pitfall traps provide a convenient method of investigating the ecology of ground invertebrates (35): our traps consisted of plastic jars (11 cm deep with a diameter at the mouth of 7 cm) sunk in the ground with their rims level with the soil surface. To prevent the runoff of water in the traps, we placed canopy stones above them. According to Szysko (36), we utilized ethylene glycol as a preserving agent, because this liquid is less volatile than formalin, and does not cause decolourization of invertebrates or stiffening of the animals and is not harmful for the operator.

Ground macro-invertebrates collected with pitfall traps were determined at species level for Carabidae, Araneidae, Orthoptera, and Dermaptera, at genus level for Gastropoda and at family level for Chilopoda, Diplopoda, Crustacea, other Coleoptera, Heteroptera and Lepidoptera (Appendix II).

Statistical analysis

We used four parameters to compare soil-extracted communities: N (number of microarthropods in the soil sample), S (number of taxa), the Shannon's biodiversity index and the Biological Soil Quality (BSQ) index. The BSQ index is based on a life-form approach: life forms include groups of microarthropods with the same convergent morphological features, and life forms more sensitive to soil quality are given a higher score (37, 38). The index is computed for each sample as the sum of scores given to all microarthropods extracted in the funnel.

For the comparison of pitfall-collected invertebrate communities, we analyzed three parameters: total number of individuals (N), taxonomic richness (S) and Shannon's biodiversity index.

We utilized multivariate models to compare communities found in the three patches, with abundance, richness and biodiversity as the dependent variables, the patch pollution and distance from the border as factors, and date as covariate. Statistics were computed by Systat 8.0 (39). Species abundance and richness values were log-transformed to reach normality. Moreover, we used an ordination technique, the Principal Component Analysis, to explore the relationships between the same variables (40, 41).

Richness accumulation curves, generated with EstimateS 6.0 software (42), were used to compare the sampling dates and cumulative taxa number for all samples from each habitat type.

The habitat preference of individual taxa was evaluated using indicator species analysis computed by the INDVAL 2.0 software (43). Indicator species analysis is a randomisation-based test that compares the relative abundance, fidelity, and relative frequency of occurrence of

TABLE 1

Edaphic fauna: comparison of community descriptors among 72 samples collected in patches with three different pollution levels (NO, LOW, HIGH), and three distances from the patch center (center, middle, edge). Time spans from 0 to 40 days after sterilization.

Dependent variable	MANOVA independent variables					
	Patch pollution		Time		Distance	
	$F_{2,66}$	P	$F_{1,66}$	P	$F_{2,66}$	P
Density (N)	16.2	<0.001	15.2	<0.001	0.45	0.64 n.s.
Taxonomical richness (S)	12.0	<0.001	15.9	<0.001	0.43	0.65 n.s.
Biodiversity index (H')	1.87	0.16 n.s.	8.35	<0.005	0.17	0.85 n.s.
BSQ index	12.9	<0.001	33.4	<0.001	0.38	0.69 n.s.

taxa to find indicator species assemblages characterizing groups of samples. A taxon's affinity for a sampling group is expressed as a percentage (43).

RESULTS

In total, we captured 3527 edaphic micro-arthropods and 5839 ground macro-invertebrates.

Pedofauna

We analysed 89 soil samples (17 in the control area and 24 in each experimental patch), collected on 6 different dates (occasions): before sterilization, 8 h, 10 days, 15 days, 25 days and 40 days after sterilisation. Mean densities before sterilisation were 103.0 microarthropods/dm³ \pm 23.6 se. No active microarthropods were collected 8 h after sterilization in the three patches.

Table I reports the results of a multivariate analysis of variance (MANOVA) with N (number of microarthropods in the soil sample), S (number of taxa), the Shannon's biodiversity index and the Biological Soil Quality (BSQ) index as dependent variables, the patch pollution level (NO, LOW, HIGH) and the distance from the edge (near, 1 meter, centre) as factors, and the elapsed time as covariate.

The three experimental patches significantly differed in N, S, H' and BSQ values (Table I). The variables were considerably lower for the highly polluted patch, attained intermediate values in the low polluted patch, and were higher in the non polluted patch (Figure 2). Community descriptors were significantly different over time (Table I), with a general trend of increase in the first 25 days, and stabilization in the last period (Figure 2). The distance from the edge did not significantly influence any dependent variable.

The final microarthropod abundances assessed in the LOW and HIGH polluted patches were only 26% and 52%, respectively, in comparison to the NO patch values. In addition, the taxonomical richness was considerably lower in the HIGH and LOW pollution patches (41% and 56% respectively). The values recorded in the control C area ($N = 83.9 \pm 16.4$ ind./dm³, $S = 7.0 \pm 0.39$ taxa,

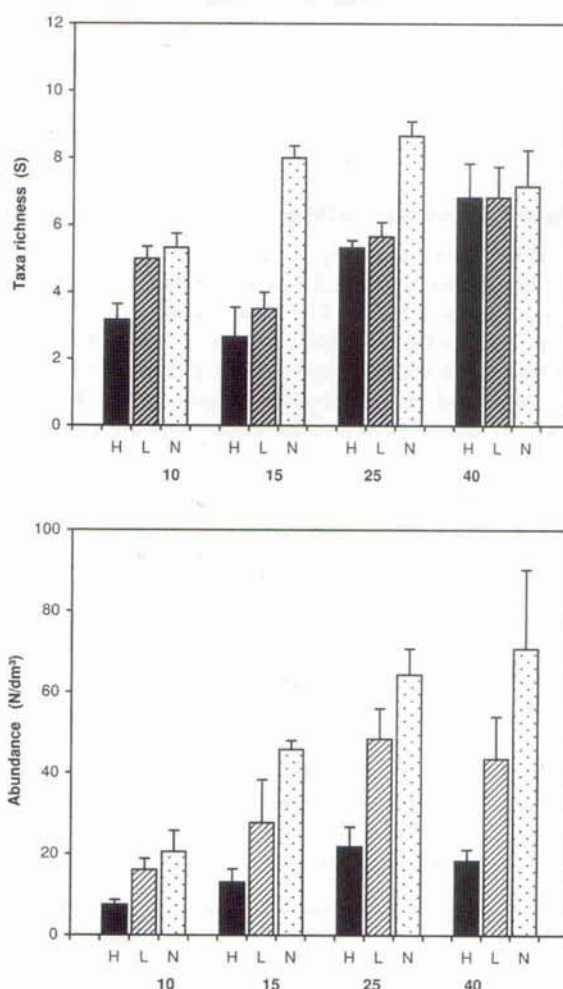


Figure 2. Abundance and taxa richness (mean \pm se) at different times of soil microarthropods sampled in three patches with different pollution levels.

$H' = 1.44 \pm 0.12$, and $BSQ = 67.3 \pm 6.8$ scores) were similar to those attained in the NO patch (abundance: $F_{1,25} = 0.62$, $P = 0.44$ n.s.; taxa richness: $F_{1,25} = 0.004$, $P = 0.95$ n.s.; Shannon index: $F_{1,25} = 0.03$, $P = 0.87$ n.s.; BSQ index: $F_{1,25} = 1.72$, $P = 0.20$ n.s.).

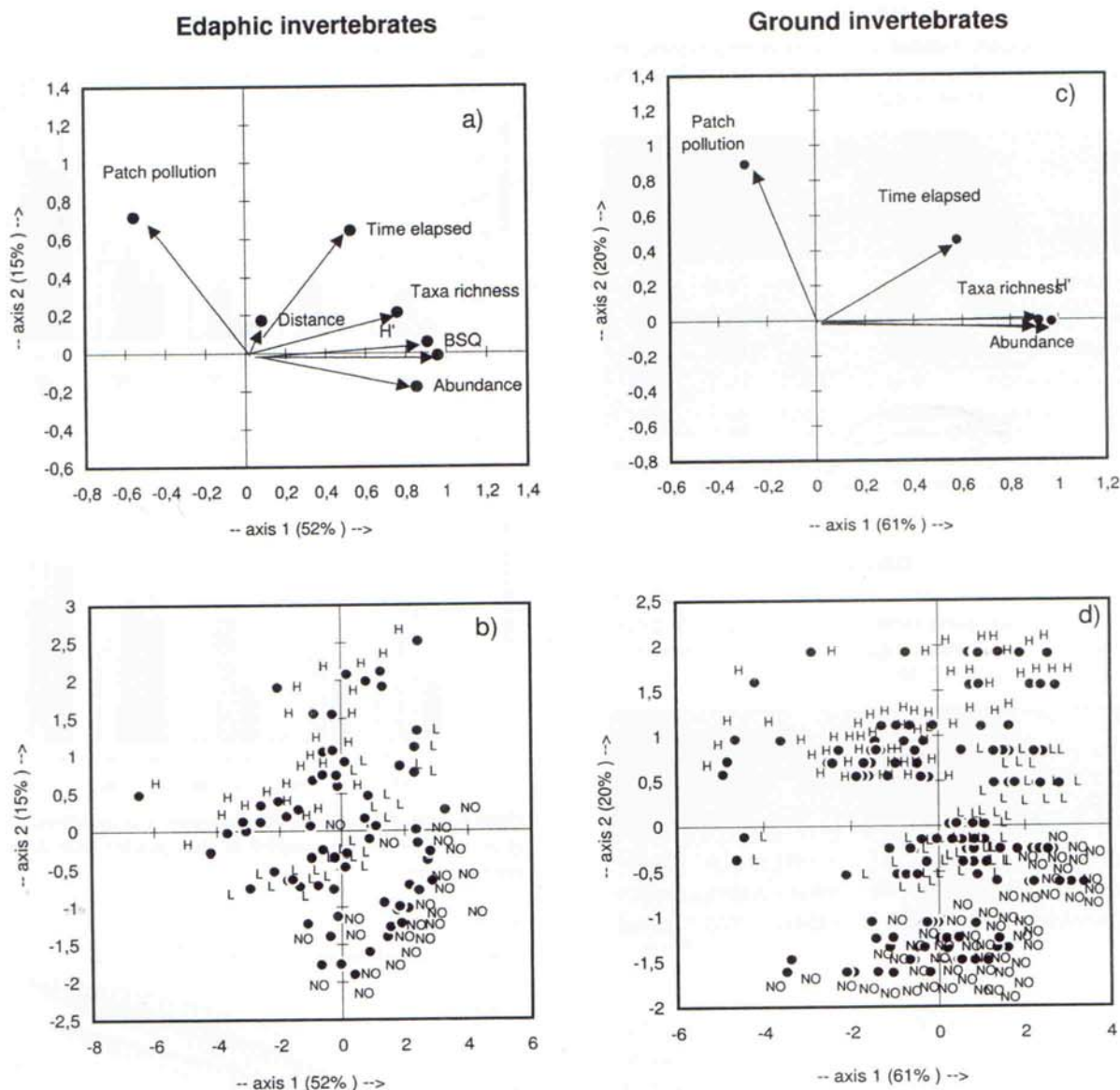


Figure 3. Biplot of the first and second Principal Component Analysis axes for the edaphic (a) and ground (c) taxa, and edaphic (b) and ground (d) samples.

Principal Component Analysis was utilized to explore the relationships between the four community descriptors and pollution level of the patch, time and distance from the edge. Factor 1 explained 52% of variance and was positively related to elapsed time and community descriptors (Abundance, Taxa richness, H' and BSQ), and negatively to patch pollution (Figure 3a). Samples were clearly scattered according to the pollution level of each patch (Figure 3b).

Analysing the taxonomical composition of edaphic communities in the patches with different pollution levels, the Indicator Species Analysis identified five sensitive taxa (Oribatida and non-Oribatida mites, Entomobriomorpha springtails, larvae of Coleoptera and Diptera), showing a statistically significant preference for the unpolluted patch.

Ground macro-invertebrates

We analysed 194 pitfall traps (28 in the control area, 55 in the H patch, 55 in the L patch, and 56 in the NO patch), collected before sterilisation, 10 days, 15 days, 25 days, 30 days and 40 days after sterilisation. Mean abundance before sterilisation was 72.7 ground invertebrates/trap \pm 6.02 se, and richness 18.8 taxa/trap \pm 0.83 se. No active ground invertebrates were collected 8 h after sterilization in the three patches.

Table 3 reports the results of a multivariate analysis of variance (MANOVA) with N (number of invertebrates/trap), S (number of taxa), and Shannon's biodiversity index as dependent variables, the patch pollution level (NO, LOW, HIGH) as factor, and the elapsed time as covariate. The three experimental patches significant-

TABLE 2

Indicator values, habitat abundance and fidelity for edaphic invertebrates collected from NO, LOW and HIGH pollution patches.

Taxa	Indicator value (%)	Pollution level (*)		
		No	Low	High
Unpolluted patch taxa				
Oribatida	44.39	114/24	99/20	42/14
Non Oribatida	53.87	564/24	366/23	112/19
Entomobriomorpha	41.10	159/17	90/16	24/12
Diptera (larvae)	38.63	23/17	15/ 7	4/ 3
Coleoptera (larvae)	37.61	60/18	20/ 9	38/14

(*) The data show the total number of individuals collected and the number of sites where each single taxon was found.

TABLE 3

Ground fauna: comparison of community descriptors among 166 samples collected in patches with three different pollution levels (NO, LOW, HIGH). Time spans from 0 to 40 days after sterilization.

Dependent variables	MANOVA independent variables			
	Patch pollution		Time	
	F _{2,161}	P	F _{1,161}	P
Density (N)	8.7	<0.001	52.6	<0.001
Taxonomical richness (S)	9.9	<0.001	40.8	<0.001
Biodiversity Index (H')	8.4	<0.001	27.3	<0.001

ly differed in N, S and H' values (Table 3). All variables showed considerably lower values in the highly polluted patch, while both the NO and the LOW polluted patches had higher values (Figure 4). Community descriptors were significantly different over time (Table 3), with low values in the first 30 days, and a conspicuous increase in the last sampling period (Figure 4).

The final invertebrate abundances assessed in the LOW and HIGH polluted patches were only 66% and 72%, respectively, in comparison to the NO patch values. In addition, the taxonomical richness was lower in the HIGH and LOW pollution patches (76% and 92% respectively). The abundance and richness values recorded in the control C area ($N = 181.6 \pm 32.0$ individuals/trap, and $S = 17.3 \pm 1.20$ taxa) were significantly higher than those attained in the NO patch (abundance: $F_{1,9} = 5.68$, $P < 0.04$; taxa richness: $F_{1,9} = 9.73$, $P < 0.012$), while Shannon index ($H' = 1.76 \pm 0.03$) did not show significant difference ($F_{1,9} = 0.13$, $P = 0.72$ n.s.).

Principal Component Analysis was utilized to explore the relationships between time, pollution level of the patch, and the three community descriptors. Factor 1

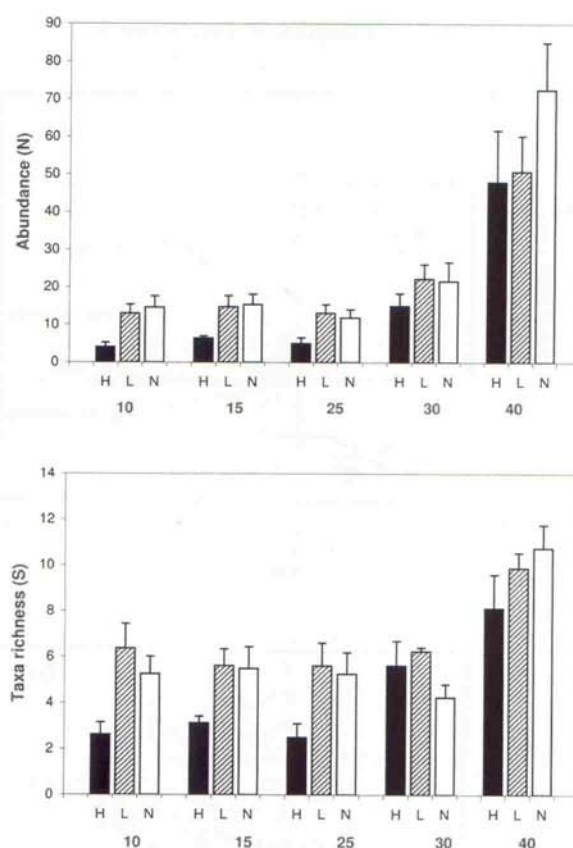


Figure 4. Abundance and taxa richness (mean \pm se) at different times of ground invertebrates sampled in three patches with different pollution levels.

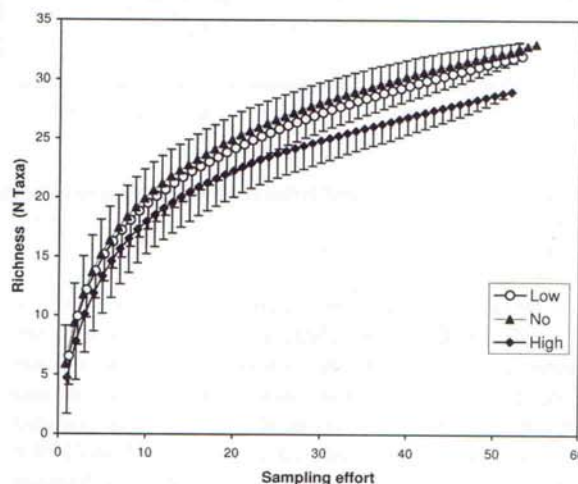


Figure 5. Taxa accumulation curves for ground invertebrates in the HIGH, LOW and NO pollution patches.

explained 61% of variance and was positively related to elapsed time and community descriptors (abundance, taxa richness, and H'), and negatively to patch pollution (Figure 3c). Pitfall samples were clearly scattered according to the pollution level of each patch (Figure 3d).

Analysing the taxonomical composition of ground communities in the patches with different pollution levels, the Indicator Species Analysis identified four more tolerant and three sensitive taxa. Some taxa promptly reappeared in the less polluted areas, such as Formicidae and some Carabidae (*Poecilus cupreus*, *Harpalus affinis*, *Anisodactylus signatus*). Other taxa were less tolerant, and appeared mainly in the unpolluted patch, such as *Pseudophonus rufipes* (Carabidae), Laemophloeidae (Coleoptera, Cucujoidea) and the spider *Pardosa torrentum* (Table 4).

Species accumulation curves showed that few additional taxa were likely to be found with additional sampling (Figure 5). The curves agree with the other data that the highly polluted patch had the lowest taxa richness.

DISCUSSION

Key aspects of resilience are the ability of a species to recolonize disturbed areas and the survival of a species in the face of disturbance (44). In our study, we investigated the first aspect, examining the reorganization patterns of invertebrate communities after total depletion and in different degrees of soil pollution. The re-establishment of fauna in terrestrial systems is an interesting subject that has been investigated for many years (45), although most studies have been conducted in artificial substrates and laboratory conditions (1, 46) or focused on/concerned with particular environmental conditions, such as the presence of compost (20), metal pollution (21) or different pH levels (47), or focused on specific taxonomic groups (48).

Our work is related to an open-field experiment, based on the colonisation process of the whole ground and edaphic invertebrate communities in different levels/degrees of pollution: because of the enormous taxa richness of these coenoses, this approach seems to be the most promising in ecological assessment of terrestrial systems (14).

Our data on the recolonization patterns underline the great resilience of soil and ground invertebrate communities in natural conditions and in the absence of contamination. Our study shows that the dispersal rate of terrestrial invertebrates is strongly related to the presence of a pollution gradient: our sampling design demonstrates that high contamination levels inhibit the re-establishment of faunal communities, and that also low contamination levels reduce the entire re-invasion process. We detected a similar pattern of recolonisation and a similar response to pollution in both ground and edaphic communities: above and below terrestrial systems are highly coupled (49) and show a similar pollution-dependent re-invasion rate. The pollution level of patches influenced both density and richness of the incoming communities. During each sampling, the abundance (number of individuals/sample) and taxonomic richness (number of taxa/sample) were noticeably lower in the highly polluted than in the non-polluted patch. Furthermore, the patch with a low level of contami-

nation was quickly colonised by truly edaphic fauna rather than ground invertebrates. In this patch, abundance and richness of soil microarthropods were similar to those reached in the unpolluted patch. Probably the sprayed chemicals showed great persistence on the surface and did not penetrate deeper into the soil. Only in major concentrations (highly polluted patch), was the effect of chemicals evident also in the truly edaphic environment.

Dispersal, i.e. the spreading of a population from one site to others, is important in demographic and evolutionary dynamics of populations (50). It is a complex process, dominated by many behavioural (22) and environmental (51) elements. However, few studies have analysed the pattern of this process at a community-level in the field. The sparse information available comes from studies focused on the impact of pollution on selected species (52). In this study, we provide synthetic data on the effect of soil contamination during recolonisation, a less known dispersion-related process. We found that the concentration of chemicals shapes the entire colonisation process, and can limit the effectiveness and/or speed of the community re-establishment. However, the recovery was to some extent rapid, and after a few weeks, the parameters describing the invertebrate community were similar in the different patches. Probably, this finding is related to the high biological diversity, a key component of ecological resilience. Soil communities are known to be the most species-rich components of terrestrial systems (53, 54) and many ecologists have suggested that in soils many species in the ecosystem are »redundant« in the sense that their contribution to the ecosystem process can be taken over by other functionally similar species (55). Another important element on the basis of the rapid rehabilitation capacity of soil coenosis is that edaphic and ground invertebrate populations show high growth rates and constitute communities with few trophic levels: these elements are known to be important to improve resilience (56).

The information provided in this study can be of interest in the assessment of the effectiveness of reclamation activities. Temporal changes in biological assemblages evidently indicate the direct effect of chemical presence on the accessibility of patches. Knowing in which way the (residual) presence of pollutants could affect the re-establishment of the invertebrate community in restored areas could be essential for measuring the efficacy of the recovery process. Restoration projects require follow-up evaluations to determine their success, and the study of a colonisation process can represent an important component of these evaluations.

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APPENDIX 1

Percent relative abundance for edaphic microarthropods collected in the Control, NO, LOW and HIGH patches (see Methods section for details). Taxonomic assemblages according to BSQ method.

Taxon	Control area	Pollution level		
		High	Low	No
Oribatida	13.3	12.9	9.82	5.06
Other Mites	35.4	47.8	48.6	48.7
Araneidae	0.32	0.52	0.26	0.16
Symphyla	0.95	1.96	1.64	0.16
Diplopoda	0.00	0.00	0.17	0.00
Chilopoda	0.63	0.00	0.00	0.23
Paupoda	0.00	0.13	0.17	0.00
Poduromorpha	9.18	9.92	9.04	19.4
Entomobriomorpha	7.59	11.7	13.7	14.8
Sympleleona	0.00	1.17	0.69	0.70
Neelipleona	1.58	0.00	0.00	0.00
Coleoptera	4.43	3.13	3.88	0.00
Hemiptera	6.96	1.44	2.33	4.60
Hymenoptera	0.95	0.39	1.21	0.00
Psocoptera	4.11	4.05	1.12	0.00
Thysanoptera	0.32	0.00	0.00	0.00
Dermaptera	0.00	0.00	0.26	0.08
Diptera (larvae)	1.27	1.96	1.98	1.56
Coleoptera (larvae)	12.0	2.61	5.17	4.52
All taxa (N =)	316	766	1161	1284

APPENDIX 2

Percent relative abundance for ground invertebrates collected in the Control, NO, LOW and HIGH patches.

Taxon	Pollution level			Control area
	High	Low	No	
Pieridae	0.90	0.42	0.81	0.79
Formicidae	14.3	18.8	14.1	14.9
<i>Gryllus campestris</i>	3.37	2.10	3.85	2.54
<i>Pyrrochoris apterus</i>	0.11	0.08	0.07	0.04
Other Hemiptera	0.56	1.01	0.22	5.20
<i>Forficula auricularia</i>	0.00	0.42	0.15	0.50
Anthicidae	25.4	22.5	22.5	9.06
Laemophaeidae	16.6	7.71	10.5	5.99
Micetophagidae	6.07	3.60	2.67	2.83
Scarabaeidae	0.00	0.25	0.37	2.70
Dermestidae	0.45	0.34	0.30	6.19
Staphilinidae	1.91	1.42	1.85	2.00
<i>Abax continuus</i>	0.00	0.00	0.00	0.46
<i>Amara aenea</i>	0.00	0.08	0.07	0.79
<i>Anchomenus dorsalis</i>	0.00	0.00	0.00	0.29
<i>Anisodactylus binotatus</i>	0.00	0.17	0.00	0.46
<i>Anisodactylus signatus</i>	1.12	2.85	0.67	1.25
<i>Brachynus explodens</i>	0.00	0.00	0.00	1.16
<i>Carabus granulatus interstitialis</i>	0.00	0.00	0.07	0.12
<i>Carabus italicus</i>	0.11	0.00	0.00	0.04
<i>Chlaeniellus nitidulus</i>	0.11	0.08	0.00	0.50
<i>Cilindela germanica</i>	0.00	0.00	0.07	0.04
<i>Harpalus affinis</i>	0.90	1.51	0.52	1.79
<i>Harpalus distinguendus</i>	0.00	0.08	0.07	0.04
<i>Platysma melanarium</i>	0.22	0.00	0.07	0.62
<i>Platysma nigrum</i>	0.00	0.00	0.07	0.33
<i>Poecilus cupreus</i>	3.60	9.22	7.48	6.44
<i>Pseudophonus rufipes</i>	13.8	19.4	24.0	22.8
<i>Pseudophonus griseus</i>	0.00	0.00	0.22	0.21
<i>Metallina</i> sp.	3.15	2.93	1.85	1.66
Silphidae	0.00	0.00	0.00	0.25
<i>Arion</i> sp.	0.00	0.00	0.00	1.00
Oniscidae	0.22	0.00	0.07	0.33
Lithobiidae	0.11	0.00	0.00	0.08
Tulidae	0.11	0.00	0.00	0.00
<i>Micaria pulicaria</i>	0.11	0.08	0.00	0.62
<i>Erigone dentipalpis</i>	0.00	0.17	0.30	0.00
<i>Meioneta rurestris</i>	0.22	0.17	0.00	0.00
<i>Odeothorax apicatus</i>	0.00	0.17	0.30	0.87
<i>Ostearius melanopygius</i>	0.11	0.00	0.00	0.00
<i>Pardosa torrentum</i>	1.46	2.18	3.19	0.42
<i>Pardosa proxima</i>	1.46	0.59	1.19	1.37
<i>Pardosa</i> sp.	1.12	0.84	1.41	1.12
<i>Trochosa ruficola</i>	1.24	0.42	0.44	1.62
<i>Scytodes thoracica</i>	0.00	0.00	0.00	0.08
<i>Xysticus cristatus</i>	0.00	0.08	0.07	0.00
<i>Zodariion italicum</i>	0.00	0.08	0.00	0.00
Opiliones	1.12	0.08	0.37	0.54
All taxa (N ind.)	890	1193	1350	2406